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Altwegg, R ; Ringsby, T H ; Seather, B E

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DOI: <https://doi.org/10.1046/j.1365-2656.2000.00431.x>

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ZORA URL: <https://doi.org/10.5167/uzh-522>

Journal Article

Published Version

Originally published at:

Altwegg, R; Ringsby, T H; Seather, B E (2000). Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology*, 69(5):762-770.

DOI: <https://doi.org/10.1046/j.1365-2656.2000.00431.x>

Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*

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Summary

1. We examine causes and consequences of natal dispersal within a metapopulation of house sparrows *Passer domesticus* in an archipelago in Northern Norway where a large proportion of the individuals is colour-ringed.
2. Less than 10% of the fledglings dispersed, i.e. left their natal island.
3. Dispersal was female biased and almost exclusively performed by juveniles.
4. The probability of natal dispersal was not related either to the body condition or the body mass of the juvenile. Similarly, neither clutch size nor hatching date explained a significant proportion of the variance in the probability of dispersal.
5. The probability of male natal dispersal was related to the rank of the fledgling in the size-hierarchy within the brood. Low ranking individuals that hatched early in the season were more likely to disperse.
6. In both sexes, the survival of dispersers at the island of establishment was higher than among the residents on that island. Similarly, dispersers survived better than adults that remained on their island of birth.
7. These results suggest that dispersal may be an adaptive strategy to avoid poor conditions in the natal area.

Key-words: dispersal, house sparrow, *Passer domesticus*, phenotypic variation, survival.

Journal of Animal Ecology (2000) **69**, 762–770

Introduction

Dispersal is one of the most important processes in population ecology which strongly influences population dynamics at both a local and regional scale (Hanski & Gyllenberg 1993; Goldwasser, Cook & Silvermann 1994; Doebeli 1995; Stacey, Johnson & Taper 1997) as well as the spatial variation in genetic composition (Ehrlich & Raven 1969; Slatkin 1985; Slatkin 1987; Holt 1996; Barton & Whitlock 1997). In birds and mammals, individual variation in dispersal behaviour is related to sex (Wolff & Plissner 1998; Dobson 1982; Liberg & von Schantz 1985; Johnson 1986; Pusey 1987; Johnson & Gaines 1990; Clarke, Sæther & Røskoft 1997) or age (Greenwood & Harvey 1982). There is also evidence that time of birth (Dhondt & Hublé 1968; Nilsson

1989), body size (Fleischer, Lowther & Johnston 1984), and clutch size (Pärt 1990) may influence variation in individual dispersal behaviour. Dispersal has also been found to be affected by processes within the natal population, such as population density (Greenwood, Harvey & Perrins 1979; Nilsson 1989), availability of good quality territories (Newton & Marquiss 1983; Stacey & Ligon 1987), or dominance status that a certain individual can achieve within the natal population (Dhondt 1979).

Some evidence suggests that dispersal imposes a cost on the dispersing individuals. The dispersal event itself may be costly in terms of energy expenditure or increased mortality (Waser, Creel & Lucas 1994). Settlement in a new population could imply costs of establishment in a new social environment or disadvantages due to the unfamiliarity with the new home area. In spite of these presumed costs, there are in almost every population some individuals that disperse (Baker 1978).

Two classes of models are commonly used to predict patterns of dispersal (Diffendorfer 1998). In the

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first type of model, dispersal occurs as a consequence of processes acting at the population level. For instance, if the growth rate of a local population within a metapopulation is positive, a surplus of individuals may be forced to emigrate to surrounding areas. Such a source population (Pulliam 1988) may help to maintain surrounding populations in suboptimal habitat with negative population growth rates (sinks). In this case, dispersal is predicted to be performed mainly by subordinate individuals which 'make the best of a bad situation'. They should do worse than philopatric individuals. Accordingly, several studies have demonstrated that dispersers have lower fitness than residents (Greenwood & Harvey 1976; Newton & Marquiss 1983; Jones 1986; Pusey & Packer 1987; Pärt 1990; Pärt 1991; Pärt 1994; Verhulst & van Eck 1996). The second class of models explores which conditions will make dispersal advantageous for the individuals such that genotypes having the option to disperse are selected for. Extensive modelling (McPeck & Holt 1992; Holt 1985; Doebeli & Ruxton 1997; Doncaster *et al.* 1997; Lemel *et al.* 1997; Kindvall 1999) has shown that evolution can lead to a non-zero dispersal rate under various conditions (see Dieckmann, O'Hara & Weisser (1999) for a review). In such cases, dispersal should be associated with benefits in terms of subsequent fitness gains that balance the costs imposed by the dispersal event. Possible benefits could be the acquisition of a better territory (Larsen & Boutin 1994), reduced competition for resources or mates (Dobson 1982) or avoidance of costs of having inbred offspring (Pusey 1987).

A general conclusion that appears from several models is that it is advantageous for some individuals to disperse but not for others (Lidicker & Stenseth 1992). Accordingly, several studies of both birds and mammals have shown that dispersal can be associated with increased survival (Johnson & Gaines 1987; Clobert *et al.* 1988; Larsen & Boutin 1994; Spear, Pyle & Nur 1998; but see Johannesen & Andreassen 1998; Aars, Johannesen & Ims 1999 and Aars & Ims, 2000), or increased reproductive success (Nilsson 1989; Rutberg & Keiper 1993; Tannerfeldt & Angerbjörn 1996; Spear *et al.* 1998), compared to the resident part of the population (see Bêlichon, Clobert & Massot (1996) for a review).

The mechanisms influencing the probability of dispersal may in this way strongly affect the dynamics of metapopulations (e.g. Sæther, Engen & Lande 1999a). Thus, such knowledge is important for predicting consequences of habitat fragmentation. Here, we present data on dispersal within a naturally fragmented population of house sparrows (*Passer domesticus* L.) in an archipelago off the coast of northern Norway. Because most of the individuals were colour-banded as fledglings or juveniles, the pattern of movement among islands is

known relatively exactly for the majority of juveniles. Thus, we avoid a common source of error in many studies of dispersal, i.e. that the probability of discovering a disperser strongly decreases with distance from the birth place (Clarke *et al.* 1997).

In this study, we examine the following questions.

1. Are there sex- or age-specific differences in dispersal behaviour? In passerine birds, dispersal is usually found to be female biased (Greenwood 1980) and more extensive among juveniles than adults (Greenwood & Harvey 1982).
2. Is there a relationship between morphological characteristics of the fledglings or reproductive biology of the parents and variation in individual dispersal behaviour?
3. What are the fitness consequences of dispersal in terms of subsequent survival?

Methods

STUDY AREA

The study area includes 14 islands in a coastal archipelago on Helgeland in northern Norway (66°N 12'E, see Ringsby *et al.* 1999). These islands are situated between 5 and 40 km off the mainland, where the distances between neighbouring islands range from 2 to 20 km. Since autumn 1992, house sparrows have been individually marked with a numbered metal ring and a unique combination of colour rings. Most individuals were banded as fledglings or caught in mist nets as juveniles. The proportion of banded individuals was more than 60% on most islands. House sparrows are sedentary, non-migratory birds (Summers-Smith 1988). At our study site, they are closely associated with human settlement and agriculture. For a further description of this metapopulation, see Ringsby, Sæther & Solberg (1998), Ringsby *et al.* (1999) and Sæther *et al.* (1999b).

Individuals that left their natal island and settled on a different one were defined as dispersers. Since we often did not know the fate of the individuals that disappeared during their first winter, only data on birds that were known to have reached an age of at least 6 months were included in the analyses.

CHARACTERISTICS OF DISPERSERS

Fledglings

To compare dispersers and residents, we chose fledgling traits that have been found to be associated with variation in fitness: fledgling mass, fledgling size, fledgling condition, clutch size, hatching date and rank of the fledgling within the clutch (see Ringsby *et al.* 1998, 1999 for a description of methods). To obtain a single measure of structural size, the measurements of tarsus and wing length were included in a principal components analysis. The

first principal component (PC1) explained 86.6% and 85.5% of the variance in these traits in females and males, respectively. Thus, this component provides for both sexes a good estimate of overall size. As a measurement for body condition, we used the residuals of a linear regression for each sex separately of body mass on body size. Accordingly, body condition is the deviation in body mass from the expected value for a certain body size. Clutch size was estimated as the maximum number of eggs found in the nest of origin. Hatching date was defined as the date of hatching of the first hatchling of the clutch (day 1 = 1 May).

The fledglings were weighed to the nearest 0.1 g, using a 0–100 Pesola spring balance. Tarsus length and wing length were measured with a slide calliper to the nearest 0.1 mm and to the nearest mm, respectively. Mass, tarsus length and wing length were adjusted to a standardized value at the age of 10 days using a mean growth rate obtained by a quadratic regression of the trait in question on fledgling age (see Ringsby *et al.* 1998).

The relative size of the fledglings within the brood was ranked according to their body mass at 10 days of age. The largest chick was ranked as number 1, whereas the lightest was given rank number 2. We chose this type of ranking (i) to make data comparable among broods of different size, and (ii) because in many broods both the largest and the smallest chick deviated more in size from the other chicks (A. Altwegg, unpublished data).

Adults

Body mass of adults was measured to the nearest 0.1 g, using a 0–100 Pesola spring balance. To obtain a measure of body size, a principal components analysis was conducted on tarsus length, wing length, bill length and bill height. The first principal component explained 44.3% and 41.1% of the variance in these traits in females and males, respectively. Thus, the principal component represented well overall size. As in fledglings, adult body condition was expressed as the deviation from the linear regression of body mass on body size. Tarsus length, bill length and bill height were measured to the nearest 0.1 mm, and wing length to the nearest 1 mm using a slide calliper. Most of the individuals have been captured and measured many times throughout their life. To minimize the effect of possible seasonal variation within individuals, average values were used for each individual. We also corrected for a possible measurement error among different observers (see Ringsby *et al.*, unpublished).

Male house sparrows have a black throat badge which has been shown to signal social dominance (Møller 1987). Throat badge size was measured as the maximum height and breadth of the black throat area when the bird was held with its bill

pointing at a right angle to its body (Møller 1987). All measurements were taken to the nearest 1 mm using a slide calliper. Total badge size was the area covered by feathers with a black basis. Following Solberg & Ringsby (1996) and Møller (1987), it was estimated from the equation: badge size (mm^2) = $166.7 + 0.45 \times \text{badge length (mm)} \times \text{badge width (mm)}$. Visible badge size was the central area with entirely black feathers. It was estimated as height \times breadth.

SURVIVAL ANALYSES

Because some marked individuals may escape detection, 'return rates' (the proportion of released birds that is later recorded) are underestimates of survival probabilities (Lebreton *et al.* 1992). Therefore, the recapture probability P_i , the probability that an individual is recaptured at time i (given it is alive at this time), has to be taken into account in estimating true survival between two capture occasions ϕ . We used the programs RELEASE (Burnham *et al.* 1987) and MARK (White & Burnham 1999), which are especially designed to handle Capture–Mark–Recapture (CMR) data, to calculate annual survival and recapture probabilities and to compare survival of residents and dispersers (see Lebreton *et al.* 1992 and White & Burnham 1999 for a detailed description of the CMR methodology and the programs that were used).

In the analysis, the capture history data of 1115 individuals (53 female dispersers, 50 male dispersers, 424 resident females, 588 resident males) for the period 1993–98 were used, excluding local populations where no immigration or emigration had been observed. Resightings were assumed to be equivalent to recaptures.

The CMR modelling approach used here makes the two basic assumptions.

1. Every marked animal present in the population at time i has the same probability of recapture P_i .

2. Every marked animal in the population immediately after time i has the same probability of surviving to time $(i + 1)$.

In order to test whether our data met these assumptions, we first performed a goodness-of-fit (GOF) test for the general model, $\phi_i P_i$ (i.e. survival rates ϕ and recapture rates P were time dependent) using program RELEASE (Burnham *et al.* 1987). The GOF test for the whole data set was rejected (Test 2 and 3, program RELEASE: $\chi^2 = 196.76$, d.f. = 144, $P = 0.002$, data split by island, sex and dispersal status). Thus, the data showed heterogeneity that could not be explained by differences between islands, sexes, dispersal status and year. A closer inspection of the GOF test results showed that one major reason for this was that the assumption of equal survival probabilities (see above) was violated for the last 2 years on one island (Hestmannøy),

which may be related to large annual variation in age structure (cf. Sæther *et al.* 1999b). After exclusion of the data from this one island, the GOF test showed that the reduced data set no longer violated the basic assumptions of the CMR modelling approach (Test 2 and 3, program RELEASE (Burnham *et al.* 1987): $\chi^2 = 126.97$, d.f. = 127, $P = 0.48$; again data split by island, sex and dispersal status). However, both parameter estimates and relative deviances among the models change very little when excluding Hestmannøy from the analyses. Hence, we here present only results based on the complete data set.

Our main goal in this analysis was to see whether there were survival differences between dispersers and residents. We also wanted to know whether these differences were sex-specific. In addition, earlier analyses had shown that both adult survival rate and recapture probabilities may differ among islands and years (Ringsby *et al.* 1999). Accordingly, we examined the effects of dispersal status d , sex s , island i and year t on the survival probability ϕ and, similarly, the effects of island i and year t on the recapture probability P . The factors are included both as main effects and/or as interactions (Lebreton *et al.* 1992). The relative deviance was calculated as the difference in $-2\log$ (likelihood) of the current model and $-2\log$ (likelihood) of the saturated model, where the saturated model is the model in which the number of parameters is equal to the sample size (White & Burnham 1999). Thus, the deviance is a measure of the relative goodness-of-fit of each model. Nested models were compared by likelihood ratio tests (LRT) to assess statistical significance of the factors.

We started the procedure of model selection with the most parameterized model $\phi_{d*s*i*t} P_{t*i}$. We then fitted simpler models with fewer factors to the data, and compared the models using Akaike's Information Criterion (AIC, see Burnham, White & Anderson (1995) for a justification of the use of this criterion). This criterion allows us to choose the model that has fewest parameters and still acceptably fits the data, i.e. the most parsimonious model for data analysis. It was calculated as $-2\log$ (likelihood) of the model plus two times the number of estimable parameters. The model with the lowest AIC is the most parsimonious one (see Burnham & Anderson (1998) for a comprehensive description of model selection strategies).

STATISTICAL ANALYSIS

Analysis of variance was done using the procedure PROC GLM in SAS (SAS Institute Inc. 1989) to account for the unbalanced design of our samples.

In order to examine which factor influenced dispersal behaviour, we regressed dispersal status (0 = resident, 1 = disperser) on the different variables

using logistic regression techniques applying the procedure PROC GENMOD in SAS (SAS Institute Inc. 1989).

Results

SEX- AND AGE-SPECIFIC DIFFERENCES

A larger proportion of dispersers was found among females than among males (9.56% ($n = 502$) and 5.71% ($n = 666$) of the female and male fledglings dispersed, respectively; $\chi^2 = 6.24$, d.f. = 1, $P = 0.01$).

In our study population, breeding dispersal occurred only in two cases. In contrast, 79 individuals dispersed during the first year of life, i.e. before their first breeding attempt. The two individuals that dispersed as adults did not perform natal dispersal.

TIMING OF DISPERSAL

Timing of dispersal could be assessed for 38 individuals. Of these birds, 35 left their island of birth during winter and early spring before the onset of their first nesting period. Only three individuals were recorded to have moved before October of their first year of life, the time when the first birds terminated the moult of the juvenile plumage (Summers-Smith 1988; Ringsby *et al.* unpublished data). Those three involved movement to neighbouring islands.

CHARACTERISTICS OF DISPERSERS

Fledglings

The probability of dispersal of female fledglings was not significantly related either to body mass, condition, clutch size or hatching date (all $P > 0.1$). However, there was a tendency that individuals of large body size were more likely to disperse than smaller ones (logistic regression, $\chi^2 = 3.256$, d.f. = 1, $n = 102$, $P = 0.071$). Neither did the probability of dispersal differ significantly among the smallest (rank = 2, see Methods) and largest (rank = 1) fledgling within the brood ($P > 0.1$).

In male fledglings, we could again find no relationship between morphological characteristics and dispersal probability (body mass, condition, body size and clutch size: all $P > 0.15$) either when each variable was analysed separately or when included into a multiple logistic regression analysis. However, the probability of dispersal decreased with hatching date ($\chi^2 = 4.316$, d.f. = 1, $n = 135$, $P = 0.038$, intercept = 0.86, slope = -0.22). Furthermore, the smallest individuals within the brood were more likely to disperse than the largest ones ($\chi^2 = 6.3710$, d.f. = 1, $n = 69$, $P = 0.012$ intercept = 0.86, coeff. of increase = -1.50).

To account for spatial or temporal differences among the local populations, we included the factors for island and year in these analyses. However, the results remained the same.

Adults

In both sexes, there was no significant ($P > 0.1$) difference in morphology between dispersers and residents (body mass, body size and condition, as well as throat badge size measures in males).

The morphological characteristics of dispersers did not differ significantly ($P > 0.1$), either from the adults on the island of origin or from the population on the island where they established.

SURVIVAL IN RELATION TO DISPERSAL

In order to compare the probability of survival of residents to that of immigrants on a particular island, we must first find the model that best fitted our data. Our starting point was the model $\phi_{d^*s^*t^*i} P_{t^*i}$ (Table 1). This model included the effects on survival of dispersal status, sex, year and island and their interactions, and the effects on recapture probability of year, island and their interaction. Then, the recapture model and the survival model were simplified by removing the non-significant effects. On the basis of the AIC criterion, the most parsimonious models were selected (see Methods). The selected model was $\phi_{d,t,i} P_{t^*i}$, which suggests that survival differed among islands and years. This con-

firms earlier results of a study on the same populations over a shorter time period (Ringsby *et al.* 1999). The selected model also implied different survival for dispersers and residents. There was no significant difference in survival rate between the sexes (Table 1a, LRT, comparing model 1 with model 3, $\chi^2 = 0.36$, d.f. = 1, $P = 0.55$). Similarly, the interaction between sex and dispersal status was not significant, suggesting no sexual difference in the probability of survival (Table 1a, LRT, comparing model 1 with model 2, $\chi^2 = 0.71$, d.f. = 1, $P = 0.40$). However, the AIC values suggest very similar parsimony of these models (Table 1a). Dispersers had significantly higher adult survival rate than residents on the same island (Fig. 1, LRT comparing model 1 with model 5, Table 1a, $\chi^2 = 8.14$, d.f. = 1, $P = 0.004$). This was a very robust result since models that do not separate between dispersers and residents were less supported by the data (Table 1a).

Next, we examined how well dispersers survived compared with the residents of their natal island. A similar pattern appeared as in the above comparison involving the island of establishment: there was no significant effect of sex (Table 1b, LRT comparing model 10 with model 11 $\chi^2 = 0.384$, d.f. = 1, $P = 0.54$) or the interaction between sex and dispersal status (Table 1b, comparing model 11 with model 13, $\chi^2 = 0.105$, d.f. = 1, $P = 0.75$). However, adult survival differed significantly between dispersers and residents (Table 1b, comparing model 11 with model 1, $\chi^2 = 8.034$, d.f. = 1, $P = 0.005$). Thus, adult house sparrows that survived the dispersal event and man-

Table 1. Model selection of adult survival rate ϕ and recapture rate P of house sparrow in relation dispersal status d (resident or dispersing), sex s , time t , island i and their interactions. The asterisk (*) represents models where all interactions were included, whereas two-way interactions are indicated by a dot (.). In the table, the models are sorted in ascending order by their AIC values. Please notice that not all tested models are shown

	Model		AIC	No. of parameters	Deviance
(a) Dispersers compared with residents on the island of establishment					
1	$\phi_{(d,t,i)}$	$P_{(t^*i)}$	3311.285	54	905.451
2	$\phi_{(d,t,i,s,d)}$	$P_{(t^*i)}$	3312.692	55	904.743
3	$\phi_{(d,s,t,i)}$	$P_{(t^*i)}$	3313.044	55	905.095
4	$\phi_{(d,s,t,i,d,i,d,t,d,s)}$	$P_{(t^*i)}$	3318.556	66	887.191
5	$\phi_{(t,i)}$	$P_{(t^*i)}$	3319.430	53	913.596
6	$\phi_{(d,s,t,i,t,i)}$	$P_{(t^*i)}$	3324.988	79	865.602
7	$\phi_{(d,i)}$	$P_{(t^*i)}$	3325.996	48	932.809
8	$\phi_{(d,s,i)}$	$P_{(t^*i)}$	3330.198	50	932.804
9	$\phi_{(d^*s^*t^*i)}$	$P_{(t^*i)}$	3503.716	216	724.022
(b) Dispersers compared with residents on their island of birth					
10	$\phi_{(d,t,i,t,i)}$	$P_{(t)}$	3357.000	54	945.202
11	$\phi_{(d,s,t,i,t,i)}$	$P_{(t)}$	3357.048	54	944.818
12	$\phi_{(d^*s^*t^*i)}$	$P_{(t)}$	3358.737	123	795.264
13	$\phi_{(d,s,t,i,t,i,s,d)}$	$P_{(t)}$	3359.059	55	944.713
14	$\phi_{(s,t,i,t,i)}$	$P_{(t)}$	3365.083	54	952.852
15	$\phi_{(d,s,t,i,d,s,d,t,d,i)}$	$P_{(t)}$	3372.619	34	1002.236
16	$\phi_{(d^*s^*t^*i)}$	$P_{(t^*i)}$	3483.354	214	739.306

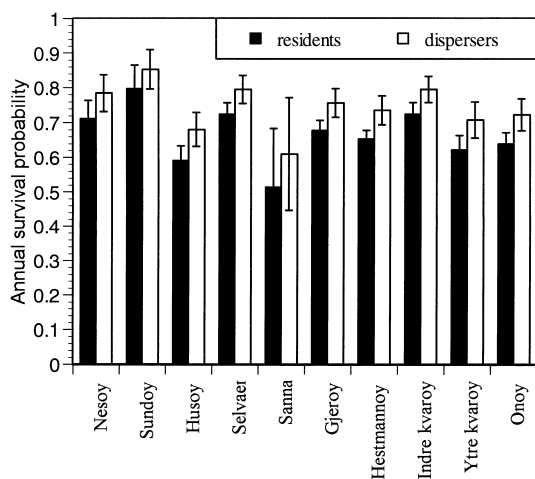


Fig. 1. The mean (\pm SE) annual survival probability of dispersing (\square) and resident (\blacksquare) adult house sparrows on the island of establishment, according to the model $\phi_{d,i} P_{r^*i}$ (see text for further explanation).

aged to establish themselves in a new local population had a significantly higher probability of survival than sedentary individuals, remaining in their natal population.

Discussion

This study confirms the general trend in passerine birds that dispersal is female-biased (Greenwood 1980; Clarke *et al.* 1997). Accordingly, female-biased dispersal has been found in other house sparrow populations as well (Fleischer *et al.* 1984). However, it was not possible in males or females to predict the probability of dispersal from either morphological characteristics of the fledgling or most of the breeding parameters of the parents. Only relative size within the clutch and date of fledging were significant predictors for male dispersal probability. However, those individuals that managed to establish themselves on a new island had a higher probability of surviving than both sedentary adults remaining on the natal island (Table 1) and adults present on the island of establishment (Fig. 1).

In this study, we define a dispersal event as emigration from one island to another. Thus, local movements within an island are not considered. This definition differs from many studies of passerine birds that have considered a smaller spatial scale in relatively continuous habitat (e.g. Fleischer *et al.* 1984; Nilsson 1989; Pärt 1990; Payne 1991; Verhulst, Perrins & Riddington 1997). Thus, differences in spatial scale in comparing dispersal distances may explain the high degree of apparent philopatry in our study. However, the house sparrow is a sedentary species (Summers-Smith 1988). Furthermore, in our study the greatest amount of natal dispersal

occurred during winter. In contrast, in other passerine species most intense dispersal has usually taken place some weeks after fledging in late summer and autumn (Dhondt 1979; Fleischer *et al.* 1984; Nilsson 1989). Again this difference may be related to the different scale of our study, and may suggest that dispersal over longer distances may occur later in the season than small-scale movements of fledglings at the end of the breeding season. In fact, this may also be due to the very fragmented structure of our landscape because increased fragmentation of suitable habitat has been found to delay natal dispersal in crested tits (Lens & Dhondt 1994) and increase dispersal distances in nuthatches (Matthysen, Adriaesen & Dhondt 1995), but decrease the probability of dispersal from the natal habitat patch in nuthatches (Matthysen *et al.* 1995) and rodents (Difendorfer, Gaines & Holt 1995).

In males, dispersal probability was related to the rank of the fledglings within the brood, i.e. the smallest individuals were most likely to move to a different island. However, no relationship was found between absolute body size and the probability of dispersal. Body size at fledging has been shown to be an important determinant for first year survival in these populations (Ringsby *et al.* 1998) as well as in other passerine birds (e.g. Tinbergen & Boerlijst 1990; Haywood & Perrins 1992). Thus, the relatively larger males within the brood with a higher chance of survival seem to be more philopatric. Similarly, Fleischer *et al.* (1984) found that, particularly among females, the smallest house sparrows dispersed the longest distances, suggesting that social interactions forced the smaller individuals to leave the area before being able to establish themselves in a flock. However, because the difference in dispersal pattern between the largest and smallest individuals within the brood was present only in males, these results suggest that those relationships are sex-specific. Thus, in order to understand the evolution of dispersal rates, possible differences in selection pressures between the sexes need to be considered. Such differences could arise from the social structure, the mating system or ecological differences and are probably responsible for sex biased dispersal rates (Greenwood 1980; Dobson 1982; Liberg & von Schantz 1985; Johnson 1986; Wolff & Plissner 1998).

Our results indicate that dispersal is a non-random process and is likely to have important fitness consequences (Table 1, Fig. 1). Dispersers of both sexes survived significantly better than residents on both their natal and establishment island (Fig. 1, Table 1), once they had established in a new population. Three interpretations may exist for these results.

1. Individuals gain fitness by dispersing and settling on sites more favourable for survival than their natal island. Such a pattern can be generated, e.g.

by differences among islands in population densities caused by asynchronous population fluctuations (see Sæther *et al.* 1999b), which is likely to influence the level of intraspecific competition, and hence the survival probability of dispersing juveniles (Both, Visser & Verboven 1999; Moorcroft *et al.* 1996). However, this mechanism cannot explain why immigrants survive better on the island of establishment than the native adults.

2. Dispersing individuals are of better quality (more viable) than residents. Even though the relatively larger male fledglings within the brood tended to be more philopatric, early born individuals were more likely to disperse than males born later in the season. We propose two mechanisms that may favour increased dispersal among early born, but relatively small, individuals. First, the probability of survival is often poor in the early part of the season (Ringsby *et al.* 1998), probably due to the adverse effects of poor weather. If the consequences for future survival are related to the size rank within the clutch, it may be favourable for the smallest individuals to leave. Secondly, the chances for the disperser to find and establish itself on an island may be higher for individuals born early in the season because early born individuals may have a competitive superiority in intraspecific competition. However, only few individuals left their island before winter (see p. 765).

3. Costs of dispersal may have greater impact on individuals of low quality, resulting in a greater survival of more viable dispersers (e.g. Tannerfeldt & Angerbjörn 1996). Currently, we lack data to examine whether any such survival cost of the dispersal event itself is involved. However, regardless of the causal mechanisms, our results suggest that development of models taking into account condition-dependent dispersal (e.g. McPeck & Holt 1992; Lemel *et al.* 1997) seem to be important for understanding the processes involved in the evolution of dispersal patterns in avian metapopulations.

Recently, several spatially structured population models have appeared (see reviews and examples in Dunning *et al.* 1995; McCullough 1996 and Hanski & Gilpin 1997) that enable us to examine the consequences of changes in the landscape structure on local and regional population dynamics. A central assumption in most of those models is that migrants and sedentary individuals can be considered as demographic equivalents. Although this may in some cases be true (e.g. Johannesen & Andreassen 1998), this study provides evidence (Table 1, Fig. 1) that dispersers have a different contribution to future population dynamics than sedentary individuals. In the present study, the higher survival rate of dispersing individuals, compared to the survival of adults on the island of establishment (Fig. 1), will increase the demographic impact of immigration on the local dynamics. The dynamic consequences of

simplifying assumptions on the dispersal process (see also Sæther *et al.* 1999a) should be quantitatively examined before making conclusions, e.g. on the risk of local extinction from analyses of models of avian metapopulations.

Acknowledgements

This study was financed by grants from the Norwegian Directorate of Nature Management and the Research Council of Norway (the 'Biological Diversity – Dynamics, Threats and Management' programme). We are grateful to A. Loison, E.J. Solberg, W.W. Weisser and two anonymous referees for helpful comments on earlier drafts of this manuscript. We thank A. Loison for invaluable help with the capture–recapture techniques and various people for assistance in the field. We also want to thank the inhabitants of Helgeland for making our field stay easy and enjoyable.

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Received 30 June 1999; received 27 November 1999